THE SIGNIFICANCE OF SCALE CHARACTERS IN EVALUATION OF THE LIZARD GENERA *GERRHONOTUS*, *ELGARIA*, AND *BARISIA*

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Abstract.— Data taken on external scale characters of 1003 specimens representing nine of the sixteen species of *Gerrhonotus* sensu Stebbins, 1958, strongly indicate that Tihen's 1949 arrangement of those species in three genera (*Gerrhonotus*, *Elgaria*, *Barisia*) is valid. Misinterpretation of the identity of the head scales in various species of this group has led erroneously to disregard of them as indicators of relationships. Actually the scales are as constant as in most other lizards and seemingly provide firm clues to natural associations.

The proper generic allocation of species of "gerrhonotine" lizards, defined as those appropriately referred to *Gerrhonotus* Wiegmann (*sensu lato*) as understood before 1942 (Smith, 1942) has remained enigmatic despite the documentation provided by the most recent review of the group by Tihen (1949), based upon osteology and external scutellation. The primary doubt was cast upon the validity of Tihen's groupings by Stebbins (1958), who proposed an alternative grouping based upon reproductive habits, color patterns, and habitat.

Haunted by the impression that external scutellation provides more reliable clues to relationships in this group than was thought by Stebbins, we initiated a re-examination of this particular aspect, utilizing materials in the University of Illinois Museum of Natural History (UIMNH), University of California Museum of Vertebrate Zoology (MVZ), University of Kansas Museum of Natural History (KUMNH), University of Michigan Museum of Zoology (UMMZ), United States National Museum (USNM), Brigham Young University Museum of Natural History (BYU), University of Colorado Museum (CUM) and University of Texas Natural History Collection (TNHC). We are much indebted to authorities at these institutions for the privilege of borrowing material from them; particularly instrumental were Dr. Donald F. Hoffmeister, Dr. Robert C. Stebbins, Dr. E. Raymond Hall, the late Dr. Norman Hartweg, the late Dr. Doris Cochran, Dr. Wilmer W. Tanner, Dr. T. Paul Maslin, and Dr. W. F. Blair. As is apparent from this list, the work here reported was completed more than a decade ago. Its results remain valid and of current interest.

Descriptive Terminology

The definition of the genera of gerrhonotine lizards requires a definitive identification of the head and body scales involved. Uniformity of terminology has not existed in the past. Indeed, misidentification of scales was important in Stebbins' (1958) rejection of scutellation as a reliable indicator of relationship. The nomenclature

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here adopted is based on the work of Tihen (1949) and Smith (1942), and was depicted first, for *Elgaria*, by Woodbury (1945).

Nasal.— The nasal scale is an unmistakable point of reference, being the anterior lateral head scale through which the external naris is pierced. It is present universally in all Gerrhonotinae, is easily found, and is difficult to misinterpret (Figs. 1, 3).

Rostral.— Except for the nasal, the rostral is the easiest to identify with certainty, being the anteriormost scale on the upper jaw. It is median and unpaired. In no specimen has it been observed split (Fig. 1).

Internasals.— Gross misinterpretations have occurred in the past simply by regarding any scales occurring between the anterior and posterior boundaries of the nasals as internasals. Unfortunately, this is not correct; such an interpretation embraces several scales in addition to the true internasals. For that reason it is best to define anterior and posterior internasals separately.

Anterior internasals.— The scales bordering the nasal anteriorly and preventing contact of the nasals with the rostral are anterior internasals. When present they occur along the posterior boundary of the rostral and may occur in one (Fig. 2) or two pairs. The anterior internasals are absent when the nasal contacts the rostral scale (Fig. 1).

Posterior internasals.— These are scales located behind the anterior internasals, or their equivalent, and along the posterior boundary of the nasals. They always are limited to the dorsal surface of the head. They too may be absent or may occur in one or two pairs (Figs. 1, 2).

Supranasals.— Scales that have as their lateral boundaries the dorsal edge of the nasals are supranasals (Fig. 2, 3, 5). They are paired or absent and take the place in some groups of the anterior internasals (Fig. 1). They may also be accompanied by both anterior and posterior internasals (Fig. 2); if so, the supranasals are posterior to the anterior internasals and anterior to the posterior internasals.

Postnasals.— The scales forming a direct posterior border with the nasal scale are postnasals (Figs. 1, 3). They are always present and occur two to a side with few exceptions. They may be designated as the upper and lower postnasals. Occasionally the upper postnasal may be in a position to be confused with the supranasal, but it can always be identified by counting the scales posterior to the nasal dorsad from their contact with the supralabials (Fig. 3).

Supralabials.— The scales bordering the upper edge of the mouth, except for the rostral. are the supralabials; they always occur in a single row in contact with the lip (Fig. 1).

Postrostrals.— One (Fig. 2) or two (Fig. 4) small azygous scales bordering the rostral at its posterior median edge are postrostrals. When two are present they form a longitudinal series.

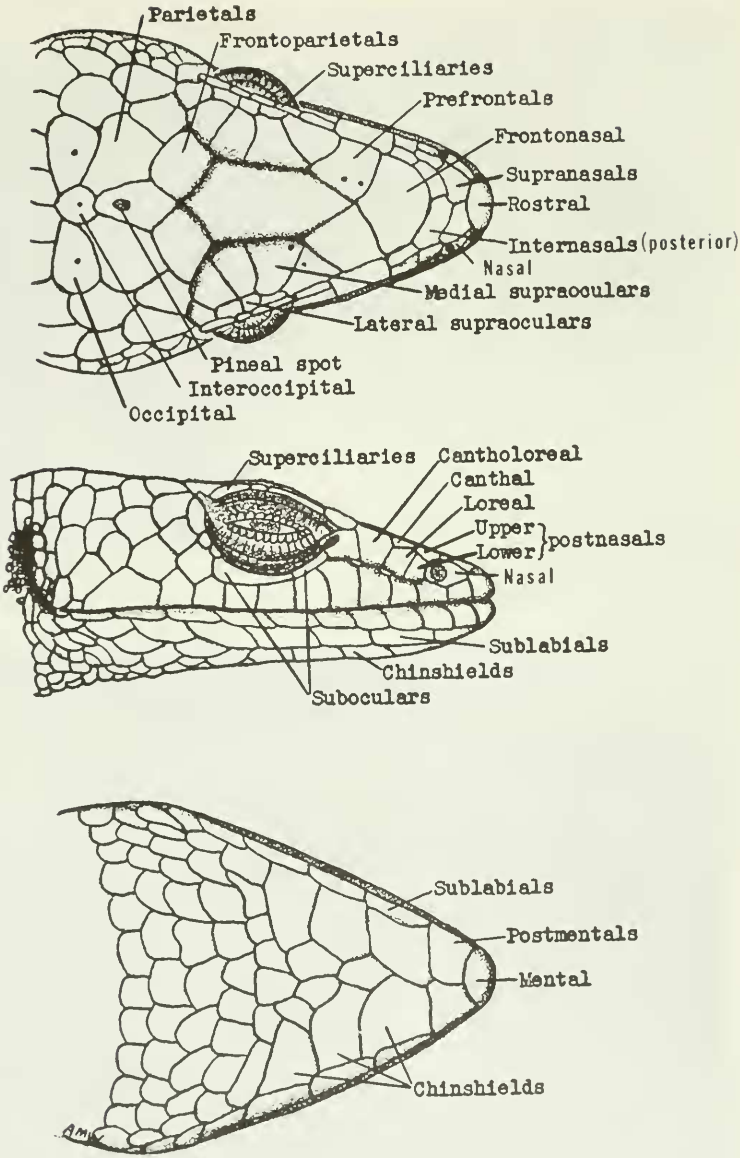

Fig. 1. Dorsal, lateral, and ventral head scales of *Elgaria coerulea shastensis* Fitch, from Woodbury (1945:10, fig 2), depicting the type of *Gerrhonotus coeruleus utahensis* Woodbury (synonymy *fide* Tanner, 1959).

Loreals.— The loreals form a series bordering the supralabials, the postnasals, the eye, and the canthals (Fig. 3). One to three may occur. They are frequently fused with the canthals, forming cantho-

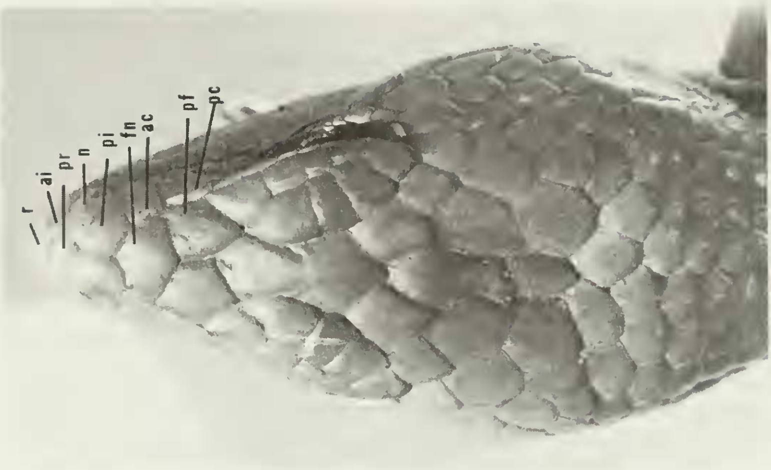

Fig. 2. Dorsal head scales of *Gerrhonotus liocephalus infernalis*, CUM 14552, Juniper Flat Road, nr. cabin area, Chisos Mts., Big Bend National Park, Brewster Co., Texas. Symbols: ac, anterior canthal; ai, anterior internasal; fn, frontonasal; n, nasal; pc, posterior canthal; pf, prefrontal; pi, posterior internasal; pr, postrostral; r, rostral.

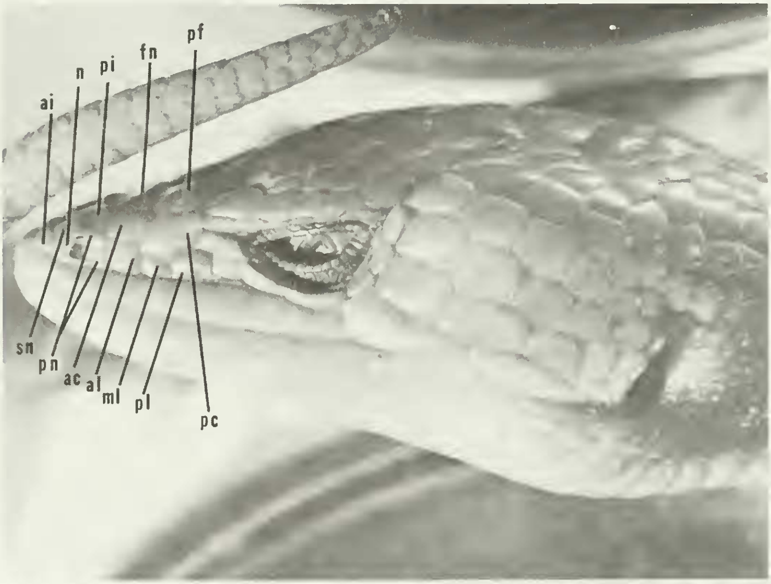

Fig. 3. Lateral head scales of *Gerrhonotus liocephalus infernalis*, CUM 14552, data as in Fig. 2. Symbols: ac, anterior canthal; ai, anterior internasal; al, anterior loreal; fn, frontonasal; ml, median loreal; n, nasal; pc, posterior canthal; pf, prefrontal; pi, posterior internasal; pl, posterior loreal; pn, postnasals; sn, supranasal.

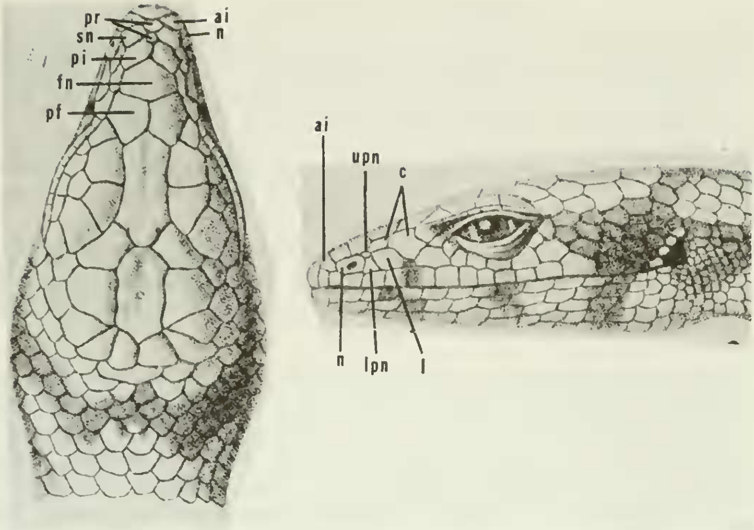

Fig. 4. Dorsal and lateral head scales of *Coloptychon rhombifer* (from Bocourt, Mission Scientifique au Mexique, Reptiles, 1878, pl. 21B, figs. 4, 4a). Symbols: ai, anterior internasal: c, canthals; fn, frontonasal; l, loreal; lpn, lower postnasal; n, nasal; pf, prefrontal; pi, posterior internasal; pr, postrostrals; sn, supranasal.

Fig. 5. Dorsal head scales of *Barisia imbricata*, CUM 48325, 21 mi. NW Galeana, Cerro Potosí, Nuovo León, Mexico. Symbols: ai, anterior internasal; pf, prefrontal; pi, posterior internasal.

loreals (Fig. 1). They are the only large scales on the sides of the snout.

Canthals.— The canthals form the peak of a ridge (the canthal ridge) separating the sides of the snout from the dorsal surface of the head (Figs. 2, 3). The scales usually occur in series with the loreals and may be fused with them (Figs. 1, 5) as cantholoreals.

Frontonasal.— The dorsal azygous scale between the canthals and posterior to the internasals is the frontonasal. It may be present (Fig. 1) or absent (Fig. 4).

Dorsal scale rows.— Counted along middorsal line from the scale behind the interparietal to the rear margins of the thigh. The number of scale rows is inversely proportional to the size of the scales.

Mental.—Directly comparable to the rostral, the mental is the anteriormost scale on the lower jaw. It too is unpaired (Fig. 1).

Chinshields.— All paired scales forming a diverging series posterior to the mental are chinshields (Fig. 1). There may be four or more pairs. The anteriormost pair cannot be mistaken for a postmental, which is always single and is not present in gerrhonotine lizards. When the anterior chinshields are anomalously fused to form a large single scale, they have a characteristic shape indicating their origin.

Gulars.— All scales noticeably smaller than chinshields and directly posterior and/or median to the chinshields are gulars (Fig. 1).

Others.— Other cephalic scales are commonly recognized and not readily subject to misinterpretation; some are illustrated and labelled on the accompanying figures.

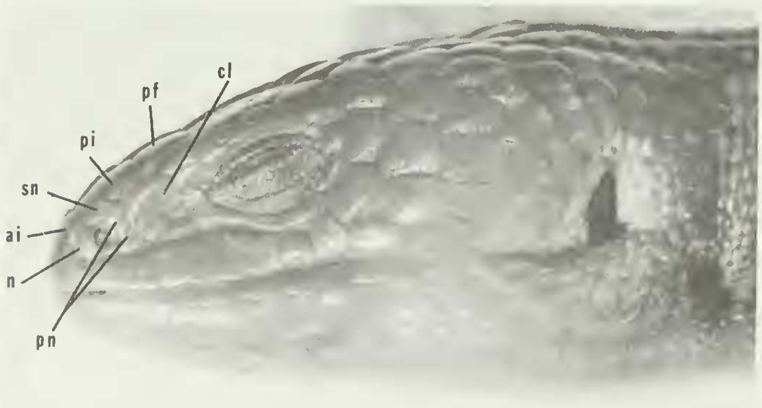

Fig. 6. Lateral head scales of *Barisia imbricata*, CUM 48325, data as in Fig. 5. Symbols: ai, anterior internasal; cl, cantholoreal; n, nasal; pf, prefrontal; pi, posterior internasal; pn, postnasals; sn, supranasal.

Materials and Methods

Utilizing over 1300 specimens that represent 33 of the species and subspecies recognized in all but the first of Tihen's five genera (*Coloptychon, Abronia, Gerrhonotus, Elgaria, Barisia*), the following data were recorded on each: postrostral(presence, absence); frontonasal (presence, absence); nasal (contacting rostral or not); loreals (number, fusion); canthals (number, fusion); anterior internasals (number, presence, absence, dorsal contact or not); posterior internasals (number, presence, absence, dorsal contact or not); supranasals (presence, absence, dorsal contact or not); dorsal scale rows (number); chinshields (single or paired); and gulars (first one single or paired).

Results

Coloptychon is a uniquely distinctive genus the validity of which is questioned by few (e.g., Wermuth, 1969). We have examined no specimens and therefore can shed no further light upon it. We call attention, however, to its unique character: two postrostrals, one following the other (Fig. 4). The genus presents no problem in an evaluation of the five gerrhonotine genera recognized by Tihen (1949).

Abronia likewise is recognized by most authorities following Tihen (1949), although not by Wermuth (1969). Although it thus constitutes no problem in the present context, we secured data on the 50 specimens of the genus available to us (Table 1). These data, and those published for the species no specimens of which we examined (*aurita, bogerti, fimbriata, fuscolabialis, matudai, mixteca, reidi, vasconcelosi*) may be summarized as follows: postrostral invariably absent; frontonasal usually present; nasal invariably separated from rostral; cantholoreals usually present; anterior internasals rarely not in contact; posterior internasals invariably in contact;

Table 1. Selected Data on Species of *Abronia*

Species and number of specimens examined	deppei (6)	lythrochila (2)	oaxacae (5)	ochoterenai (3)	taeniata (34)
Posterior internasals contact (%)	100	100	100	100	100
Frontonasal present (%)	100	100	40	100	85
Nasal separated from rostral (%)	100	100	100	100	100
Cantholoreal present (%)	0	100	100	100	85
Anterior internasals contact (%)	100	100	100	100	94
Supranasals present (%)	100	100	100	100	97
First chinshield paired (%)	100	0	100	100	100
First gular single (%)	100	100	100	100	85
Postrostral absent (%)	100	100	100	100	100
Dorsal scale rows range	27-30	33-36	28	28-33	24-29
Dorsal scale rows mean	28.4	34.5	28	30.6	26.9

supranasals rarely not present; first chinshields usually paired; first gular usually single; dorsal scale rows 24-36 (means 28-34).

The critical groups, whose validity of segregation has been widely questioned, are those designated by Tihen (1949) as the genera *Gerrhonotus*, *Elgaria*, and *Barisia*. Variation in the 1003 specimens from which complete data could be taken, representing nine species referable to these genera as of Tihen, is summarized in Table 2. These data clearly support Tihen's arrangement, which appears to reflect natural relationships. It is quite apparent that, far from being so variable as to be irrelevant, cephalic scutellation is constant within recognizable parameters in each natural group and provides vital clues to relationship. Extensive variation does exist, but it is not totally haphazard; clearly recognizable limits do exist, permitting ready recognition of natural groups.

Although we examined no specimens of four species of *Barisia* (*antauges*, *lugoi*, *modesta*, *rudicollis*) or of three of *Elgaria* (*cedrosensis*, *panamintinus*, *paucicarinatus*), the published descriptions of these taxa fall well within the range of the species we have examined. The generalizations evident from Table 3 are therefore valid for all species of these groups, although derived from the specimens we examined, representing the monotypic *Gerrhonotus*, 3 of the 6 species of *Elgaria*, and 5 of the 9 species of *Barisia*. Our series are sufficiently large to secure the validity of the indicated generalizations. Thus, *Gerrhonotus* differs trenchantly from *Elgaria* in six characters (1, 2, 3, 4, 6, 7); *Elgaria* from *Barisia* in three characters (2, 5, 6); and *Barisia* from *Gerrhonotus* in four characters (1, 3, 5, 7). Few of the individual differing character-states are absolute, but in combination they are.

We are confident that the three groups into which these 13 species fall on the basis of external scutellation are natural. The habitus of each group is also distinctive. Although Criley (1968) found no cranial distinctions, we are convinced that osteological distinctions correlated with differences in habitus will be found. Stebbins (1958), to be sure, interpreted *coeruleus* of the *Elgaria* group as a member of the *Barisia* group (subgenus *Barisia* of *Gerrhonotus*) and placed *liocephalus* with the rest of the *Elgaria* group (subgenus *Gerrhonotus*). That proposal, however, completely disregarded the scale characters here emphasized and the general habitus; it was predicated essentially upon reproductive and behavorial similarities. Those criteria, as he noted, are poorly known, and we point out that they are notoriously misleading unless fully documented. We regard Stebbins's subgenera *Barisia* and *Gerrhonotus* as artificial (through inclusion of *coeruleus* with *Barisia* and all other *Elgaria* with *Gerrhonotus*) and therefore untenable.

The scutellation data are incontrovertible in supporting the association Tihen originally proposed, and habitus is confirmatory. At the present time we are aware of no significant evidence that Tihen's five genera are not natural.

Even if admitted as natural, the validity of generic as opposed to subgeneric status of the *Gerrhonotus-Elgaria-Barisia* groups is open

TABLE 2. Variation in selected characters in species of *Gerrhonotus*, *Elgaria*, and *Barisia*

Species and number of specimens examined	liocephalus (131)	coerulea (421)	kingi (47)	multicarinata (78)	gadovi (62)	imbricata (104)	monticola (56)	moreleti (93)	viridiflava (11)
Postrostral (%)	95	7	4	5	35.5	1	0	4	9
Frontonasal (%)	98	99	98	100	100	6	100	99	55
Nasal-rostral (%)	1	98	94	100	0	0	3	1	0
Cantholoreal (%)	8	99	100	99	99	91	100	30	91
Ant. Intern. (%)	100	1	0	0	100	100	100	100	91
Ant. Intern. Cont. (%)	0	0	0	0	58	100	100	95	91
Post. Intern. (%)	100	100	100	100	100	100	100	100	100
Post. Intern. Cont. (%)	93	90	90	83	99	99	90	98	100
Supranasals (%)	100	100	100	100	100	0	73	99	100
Supranasals Cont. (%)	0	98	98	86	0	0	0	1	9
One ant. chinsh. (%)	0	0	0	0	0	0	98	98	100
Two ant. chinsh. (%)	100	100	100	100	100	100	2	2	0
One ant. gular (%)	29	97	100	100	100	95	90	87	100
Two ant. gulars (%)	71	3	0	0	0	5	10	13	0
Scale Rows	44-64	40-55	47-63	42-53	44-57	35-52	40-52	47-59	47-56
Mean Sc. R.	51	47.9	55.5	48.2	48.2	40.6	44.7	52.8	51.7

TABLE 3. Contrasts between the genera *Gerrhonotus*, *Elgario*, and *Barisia*.

Genera	GERRHONOTUS	ELGARIA	BARISIA
1. Postrostral absent	Seldom	Rarely not	Usually
2. Nasal-rostral contact	Rarely	Rarely not	Rarely
3. Cantholoreal present	Seldom	Rarely not	Usually
4. Ant. intern. present	Always	Rarely	Rarely not
5. Ant. intern. cont.	Never	Never	Usually
6. Supranasals cont.	Never	Rarely not	Rarely
7. Two ant. gulars	Usually	Rarely	Rarely

to question. The differential characters, however (even though each separately overlaps at least slightly), collectively indicate a long history of independent evolution that we regard as being consistent with separate generic status. We anticipate that ethological, serological, osteological, and karyological work in the future will substantiate these groupings and their generic rank.

It is quite evident that *Barisia* is the more variable and plastic of the three more closely related gerrhonotine genera, and it is presumably the most primitive of them. *Elgaria* and *Gerrhonotus* appear to be almost equally specialized derivatives from ancestral forms of *Barisia*, although the *imbricata* series of the latter genus is almost as specialized as the genera *Elgaria* and *Gerrhonotus*. Intermediates link all members of *Barisia*, however, whereas the members of both *Elgaria* and *Gerrhonotus* are trenchantly distinctive.

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